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The role of adult experience in nest building in the zebra finch, *Taeniopygia guttata*

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Whether learning plays a role in nest building in birds is largely unknown. Here we investigated whether the colour of nest materials used to build a first nest affected the subsequent nest material choices made by male zebra finches when building a second nest. Males were tested for their preference for green or brown nest material and then were provided with either their preferred or nonpreferred colour with which to build their first nest. The success of this nesting attempt was manipulated such that half of the breeding pairs had their eggs removed, while the other half were allowed to keep their eggs and fledge chicks. Males were then retested to determine which colour of nest material they now preferred. Males had strong initial preferences for one or other of the two colours of nest material. Males that built a nest with their preferred colour of nest material continued to prefer that colour after nesting, regardless of their breeding success in that nest. However, of the males that built a nest with material of their nonpreferred colour, those that raised and fledged chicks from it subsequently preferred that colour of material for their second nest, while males that suffered a failed breeding attempt did not. Thus breeding experience can influence decisions relating to nest material choice in nest construction in the zebra finch.

Nest building in birds often includes choosing nest materials, attaching the material to an appropriate site, and binding it all together into a species-specific structure (Collias & Collias 1984). Although this behaviour may result in a seemingly elaborate structure in many cases (Hansell 2000), it is far from clear whether learning plays a role. Indeed, it is generally considered that cognition is not involved in nest construction (Hansell & Ruxton 2008; Raby & Clayton 2009; Seed & Byrne 2010). Evidence for an unlearned predisposition for birds to build nests comes even from species that are considered to construct some of the most elaborate nests: as young chicks, male village weaverbirds, *Textor cucullatus*, deprived of nest material, attempt to weave each other's feathers (Collias & Collias 1964). However, early experience also appears to be key in developing a number of nest-building skills in this species. For example, young males that were deprived of nest materials (palm strips or reed grass) for a month were not as proficient at ripping off strands for nest building as controls that had not been deprived of these materials. When males were further deprived for a year and then provided with nest materials, they wove less frequently and produced fewer nests than did control birds. The weaving skills of these deprived males did improve with experience, but they never reached the standard of weaving shown by the control birds (Collias & Collias 1964). Like first-time builders, these males with early deprivation tended to build nests with loose loops and ends (Collias & Collias 1964) in comparison to the more tightly woven nests of adult males. Similarly, nests built by wild, free-living southern masked weavers, *Ploceus velatus*, and village weavers, *Ploceus cucullatus*, become smaller and lighter over time (Walsh et al. 2010).

In addition to changes in weaving ability with experience, male village weaverbirds become increasingly discriminating in their choice of nest material as they mature, selecting grass and avoiding the toothpicks or raffia that they choose as juveniles (Collias & Collias 1964). Experience also appears to influence the choice of nest materials and building location in the zebra finch (Sargent 1965). Captive zebra finches that were given green or brown nest material to build a nest always preferred that colour on a subsequent nesting attempt (although birds that built red nests did not later prefer red nest material). Similarly, birds offered the choice of a 'habitat' (inside or outside the cage) and 'substrate' (either a nest cup or box) preferred the habitat and substrate to which they had been allocated for nesting on their previous nesting attempt (Sargent 1965). Experience with the natal nest also appears to influence adult preferences, but to a lesser degree than does experience as an adult builder. For example, birds reared in green nests preferred green nest material more strongly than did birds reared in brown nests (Sargent 1965).

There is considerably more evidence for the effect of experience on the choice of habitat in bird nest building. Typically, birds that breed successfully in a particular habitat or type of nestbox will return to breed in the same type in subsequent seasons, while those

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that are unsuccessful are less likely to do so (for example, Herlugson 1981; Gavin & Bollinger 1988; Haas 1998; Hoover 2003). However, it is not clear whether the success of a previous breeding attempt similarly influences decisions relating to nest building, such as the type of material used or how the nest is constructed.

Here we investigated whether the success of a breeding experience would affect the subsequent choice of nest materials in zebra finches. The zebra finch is a useful species for studying nest-building behaviour logistically because it has a short generation time and breeds readily in captivity. In the wild, zebra finches typically build domed nests from dead grass stems, although large variation has been documented both in the dimensions of their nests and in the materials used to build nests, within and among colonies (Immelmann 1962 cited in Zann 1996). There is also considerable variation in their choice of nest sites, including a range of shrub and tree species, in the foundations of raptor nests (Zann 1996) as well as in nestboxes (Griffith et al. 2008). As they often suffer high levels of nest predation (Zann 1996; Griffith et al. 2008), an ability to learn to associate the success or failure of a breeding attempt with key aspects of the nest and its site could reduce the risk of predation in later nesting attempts. In our experiment, we tested males in breeding pairs for their initial preference for one of two colours of nest material shortly prior to nest building with either their preferred or nonpreferred colour. We examined only male behaviour because although both males and females manipulate nest material once it is in the nest, it is the male who takes material to the nest (Zann 1996). We manipulated the colour of nest material as colour has previously been shown to be a relevant factor in nest construction for zebra finches (Sargent 1965) and we also manipulated breeding success by allowing half of the pairs to hatch eggs and rear chicks, and removing eggs from the other half of the pairs once they were incubating a completed clutch.

If zebra finches do learn to associate the colour of nest material with their breeding success in that nest, we would predict that males from pairs that bred successfully would prefer to use the same colour of nest material for a future breeding attempt, while males from unsuccessful pairs would have a reduced preference for that colour. If, on the other hand, experience alone with a particular colour of nest material causes males to prefer that colour for a second nest, regardless of their breeding success, then initial preferences for nest material colour should change to whichever colour the male used for nesting.

METHODS

Subjects

The subjects used in this experiment were 35 male and 35 female zebra finches. All birds used were aged between 3 and 15 months of age and had been bred in captivity at either the University of St Andrews or the University of Glasgow, U.K. None of the birds had had previous experience of building a nest. Birds were kept on a 14:10 h light:dark cycle, at a temperature of 19–32 °C, with humidity levels of 50–70% and were given access to food (mixed seeds, cuttlebone and oystershell grit) and water ad libitum. Breeding pairs were provided with 1 tablespoon of Haith's Egg Biscuit Food three times a week and daily once they had chicks. All breeding pairs were also given spinach once every 1–2 weeks. When not breeding, birds were housed in single-sex cages in groups varying from six to 20 birds. When birds were paired for nesting, they were moved to wooden cages (44 × 30 cm and 39 cm high) and provided with a wooden nestbox (11 × 13 cm and 12 cm high). As the walls of their cages were wooden, pairs were prevented from seeing building by neighbouring males. Pairs may have been able to see nest building occurring in the cages across the room. If so, they would have seen green and brown nest material being used.

Experimental Protocol

None of the birds had had a previous opportunity to breed or interact with nest materials. Pairs were chosen such that they were no more closely related than first cousins and no two pairs were of the same relatedness to each other. The experiment was carried out in three blocks (Block 1, $N = 11$ pairs; Block 2, $N = 20$ pairs; Block 3, $N = 4$ pairs). In all parts of the experiment where preferences for nest material colour were tested, only the male's preference was addressed. All preference tests were recorded using Sony Handycam camcorders. The nest material used was coconut fibre and hay, as is standard procedure in our laboratory, and was dyed green and brown using food colouring (Supercook Ltd., Leeds, U.K.).

Test 1: Initial Colour Preferences

To determine whether males preferred a particular colour of nest material, pairs were presented with green and brown material after 24 h of being caged together. Birds were provided with 3 g (1.5 g each of hay and of coconut fibre) of each colour of nest material. Each colour of nest material was placed either to the far left or to the far right end of the cage on the cage floor with the nestbox hung in the centre of the back wall of the cage. The end of the cage at which each colour of nest material was placed was alternated between cages. The camcorder was focused on the nestbox and the area of the cage floor covered by the nest material, and pairs were filmed until the male had taken at least 10 pieces of material to the nestbox. The nestbox was checked by eye without any disturbance to the birds once an hour for the first 3 h and once every 2–3 h after that. After the male had added at least 10 pieces, the nestbox and all the nest material were removed from the cage.

The video data were used to determine which colour of nest material the male preferred and were analysed using software for behavioural analysis (Noldus Observer, TrackSys Ltd., Nottingham, U.K.). We considered that a male had made a 'choice' each time he took nest material of a particular colour to the nestbox and determined his preference based on the first 10 choices of material that he made. As well as recording when the male took nest material to the nestbox, we also recorded the number of times he poked both colours of nest material as an indication of his tendency to explore both colours equally. We did not see females removing nest material added by males, although in three pairs the females did all the nest building and the males did not take material to the nest. We excluded these pairs from the experiment.

Nest Building with Preferred or Nonpreferred Colour

Once all of the males' initial nest material preferences had been determined, half of the pairs were provided with the nest material of the male's preferred colour (green: $N = 14$; brown: $N = 2$) and half were provided with nest material of the male's nonpreferred colour (brown: $N = 13$; green: $N = 3$).

Nest material was provided twice a day at 0900 and 1400 hours until the first egg was laid (at around 6 days: Zann 1996). If the female did not begin to lay within 4 weeks after nest material had been provided, the pair was removed from the experiment ($N = 8$). Pairs that laid eggs but then threw them out of the nest were also removed from the experiment ($N = 3$).